Aestivation in the Land Snail *Helminthoglypta arrosa* (Binney)

(Pulmonata : Helicidae)

BY

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(1 Text figure)

INTRODUCTION

Long term dormancy during dry seasons or aestivation is a widespread phenomenon of considerable importance among pulmonates. The time spent in aestivation exceeds the time spent in activity in some snail species (Comfort, 1957). According to Kondo (1964) aestivation has been proposed as a response to dryness, heat of summer, starvation and low humidity. Evidence from my study indicates that avoidance of predation might also be an advantage of aestivation.

Helminthoglypta arrosa (Binney, 1855), a pulmonate that occurs along the north central California coast (Pilsbry, 1939) aestivates during annual dry periods (late spring to early autumn; see Elford, 1964 or van der Laan, 1971, for details of the weather pattern). I report here on the nature, frequency, and importance of aestivation and on factors affecting variation in selection of aestivation sites for a population of *H. arrosa* that inhabits a lupine scrub stand (*Lupinus arboreus* Sims) on Mussel Point, Bodega Head, Sonoma County, California (38°20′ N; 123°04′ W, about 105 km north of San Francisco).

In this report "least diameter" (hereafter LD) refers to an estimated snail size: the distance from the intersection of the right side of the aperture lip and the body whorl to the farthest point across the height of the shell.

NATURE, FREQUENCY AND IMPORTANCE OF AESTIVATION

I examined the nature, frequency and importance of aestivation in 3 series (Series A-C) of laboratory experiments and in 3 types (Types I-III) of field observations. I considered *Helminthoglypta* to be in aestivation if I could see an epiphragm in the shell aperture, or if the snails were attached by the aperture to flat surfaces, or if when left undisturbed the snails remained completely within their shells for 5 minutes or more.

LABORATORY EXPERIMENTS MATERIALS AND METHODS

I monitored the wet weight and survival of aestivating snails collected in the field in the late summers and early autumns of 1966 and 1968 (Series A and C experiments) and of active snails collected in spring 1968 (Series B). Snails were confined in crumpled up aluminum weighing pans and placed under relative humidity of $<5\%$ and typical room temperature (22° C) in a glass desiccation chamber. The procedure for checking vitality, which was similar to that used by Lynch (1966) for freshwater pulmonates, was: (1) to examine snails for any movement within the shell; (2) with no obvious movement to hold snails within the heat of a microscope lamp, for heat stimulated movement, especially heart movement, which was visible through the shells in *Helminthoglypta* less than 11 mm LD; (3) with no movement after heat stimulus to remove the epiphragm (if present) and pinprick the snails' feet; (4) with no response to pricking to (a) remove snails from the experiment, (b) place them on wet towelling in a petri dish, (c) sprinkle water on their feet, and (d) re-examine snails for activity within 24 hours; and (5) with no activity after wetting to (a) cut shells back from the aperture toward the body whorl, (b) prod or prick again and (c) record the presence or absence of a response.

In Series A I estimated the reduction in weight loss attributable to vital processes and to epiphragms by comparing weight loss in living snails with epiphragms to the loss in snails with epiphragms which were killed by freezing prior to placement in the desiccator and in living snails from which I removed the epiphragms prior to and during placement in the desiccator. The removed epiphragms, which were formed about every other day, were weighed with their respective snails.

RESULTS

Apparently some vital process increases resistance to desiccation, for in Series A the weight loss of 6 living snails averaged 5% in 3 days compared to 35 to 67% loss for 5 dead snails in the same time.

Epiphragms were also important in reducing weight loss. For example, 11 days after the start of Series A, 5 snails without and 5 with epiphragms had mean weight losses of 12.9% and 6.2%, respectively. At 78 days 2 snails without epiphragms had lost 33.7% and 34.6% compared to a mean loss of 13.2% for 4 snails with epiphragms.

Weight losses occurring during long term (30-169 days) aestivation were rapidly made up when snails were reawakened and presented free water. A 50% weight increase within 24 hours of reawakening was common.

Snails maintained dormancy for long periods of time. Eighteen Series B snails and 9 Series C snails survived 78+ days in the desiccator. In Series A 1 snail was viable after 169 days, and this snail and Series C snails were probably in aestivation at least 30 additional days since they were collected already in aestivation late in the dry season (August-September). On the other hand, some snails died as early as 8 days after the start of Series B and at 18 days in Series C. Larger animals tended more to survive the experimental conditions as indicated by a point biserial test of correlation between mean size and survival (Table 1). The activity level that snails were in when collected appeared to be not important in surviving the experimental conditions. The proportion of surviving Series B snails which were active when collected was not significantly different ($X^2 = 0.377$; $p < 0.30$) from the proportion of surviving Series C snails which were in aestivation when collected. In general, a loss of over 50% wet weight resulted in death, whereas life was maintained with up to 40% loss (Table 1).

DISCUSSION

Previous studies on pulmonates (Cameron, 1970; Machin, 1967, 1968) have shown that like in *Helminthoglypta* the epiphragm is an important structure for reducing weight loss. On the other hand, snails can survive long periods of time without epiphragms (78+ days, 0.2 years for *H. arrosa,* from 0.4 to 2.9 years for 3 species studied by Machin, 1967). Machin (*op. cit.*) also found that a loss of 35% wet weight was tolerable for pulmonate survival, which is close to my estimate of 40% for *H. arrosa.* It should also be noted that the 50% weight gain I found for reawakened snails is well within the values found for reawakened *Helix pomatia* Linnaeus, 1758 (Howles & Wells, 1934).

My laboratory study shows that large numbers of *Helminthoglypta* can maintain dormancy for a length of time (78-170 days or more) (1) which is typical for pulmonates (cf. Comfort, 1957); (2) which is as long or longer than Mussel Point's annual dry period (ca. 90 days) and (3) under conditions that are drier (<5% R. H.) than occur in the field. Since fog occurs during half of the annual dry period a relative humidity as low as 5% occurs infrequently at Mussel Point.

Table 1

Weight Losses and Sizes of Snails Surviving 78+ Days and Dying Prior to 78 Days in Series B and C Laboratory Experiments

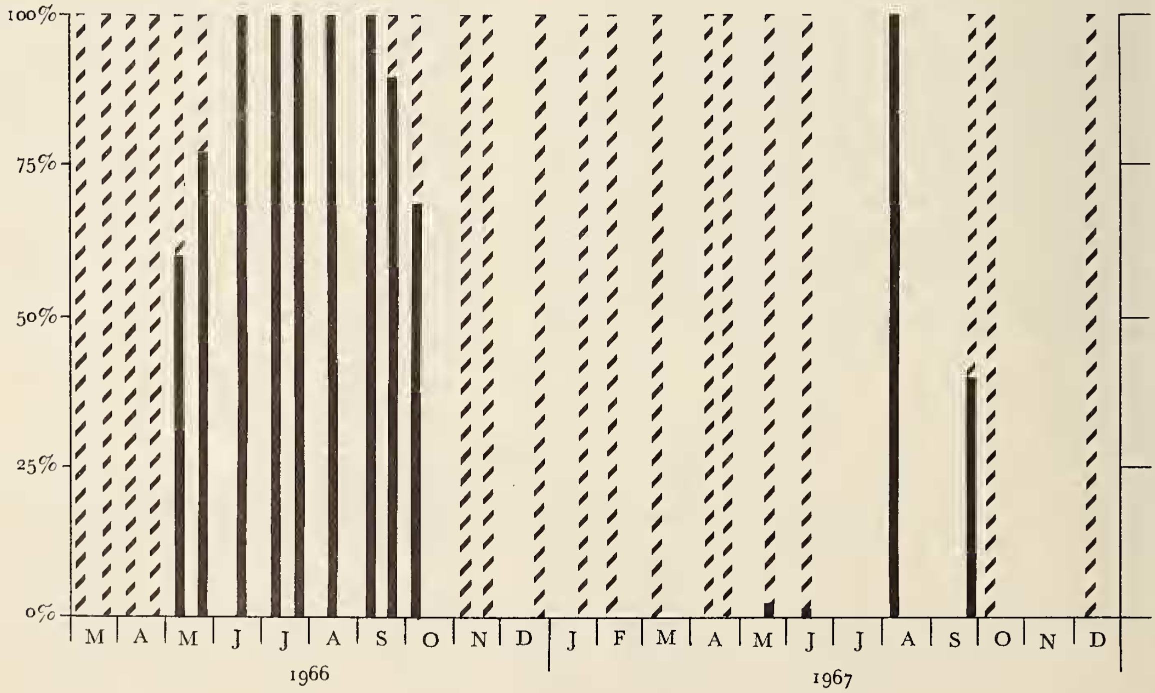
Experiment	Survivors After 78 Days	Casualties Prior to 78 Days	Σ	Mean Percent Weight Loss of Surviving Snails	Weight Range of Surviving Snails (%)	Mean Percent Weight Loss of Dying Snails	Weight Range of Dying Snails (%)	Mean Sizes ("least diameter" in mm) of Snails Surviving 78 or More Days	Mean Sizes ("least diameter" in mm) of Snails Dying by 77 or Fewer Days	Point Biserial Correlation Coefficient Between Sizes and Survival r p
B	18	14	32	30.3	4.8-52.6	57.7	6.1-78.2	4.27	2.92	0.369<0.05
C	9	10	19	17.8	7.7-30.5	48.6	10.2-66.1	6.52	2.34	0.538<0.05
B & C	27	24	51					5.28	2.68	0.442<0.05

In a laboratory study similar to mine, CAMERON (1970) found (unlike *Helminthoglypta*) significant mortality in 3 species of adult snails. On the other hand, his results correlate with the tendency for young (small) rather than older (large) *H. arrosa* to die under dry conditions since the smallest of the 3 species he studied had the lowest survival; a difference, he concluded, that was partly related to thinner shells and greater surface to volume ratios for juvenile and smaller species. The immediate cause of death in both my and his experiments probably was desiccation; however, neither controls in which snails were confined but allowed to be active and given food and water, nor controls in which snails were confined and given food only, were maintained in my or Cameron's experiments; hence declining food supply or even a container effect cannot be eliminated as the sources of mortality. In field studies other researchers have indicated the importance of both food and water in causing death in pulmonates. For example, HUNTER (1966) concluded that juvenile mortality in the slug *Milax budapestensis* Hazay was largely due to local food shortage, and BERRY (1966) found in Malayan snails that dryness increased mortality.

FIELD OBSERVATIONS

METHODS AND MATERIALS

In Type I field observations I cursorily examined the scrub study area at least semi-weekly between March, 1966 and December, 1969, for the presence or absence of aestivating *Helminthoglypta*. I observed (Type II) aestivating snails during or soon after rains and heavy fogs in the summers and autumns of 1966, 1967, and 1968. In Type III I estimated the population size and the proportion of snails in aestivation (Figure 1) every 6 weeks or less between March, 1966 and December, 1969 by examing and hand sorting the vegetation and upper 8 cm of soil for snails at randomly selected sampling sites which were usually 40 in number and predominantly 625 and 642 cm^2 in surface area.



Percentage of snails active (diagonal lines) and in aestivation (solid bars) in regular field collections (Type III)

RESULTS

I observed (Types I and III) *Helminthoglypta* in aestivation as early as April, with thin epiphragms and in all years of my study. High proportions, greater than 70% of the total number of animals in Type III, of snails were in aestivation during the drier months, mid-May to early October (Figure 1). Except for 2 instances - July, 1968 and August, 1969 - all of the snails were aestivating in July and August of each year. In contrast, no snails were in aestivation in any January, February or March of my study - Type I and III - and high proportions (greater than 70% in Type III) of snails were active during the wet months - mid-November to early April (Figure 1), except for December, 1967 and November, 1968 when snails aestivated (Type I observation) after a week's duration of clear, dry cold weather.

Based on observations of aestivating snails I collected (Type III) from May to August each year and of aestivating snails I examined during the laboratory experiments described above, I noted differences in the state of aestivation which appeared to depend on the length of time in aestivation. Comparing short versus long term aestivation, snails in long term aestivation (1) were farther withdrawn into their shells, (2) had 2 and sometimes 3 epiphragms, rather than 1, and (3) in order to reawaken the snails, it was necessary to squirt water directly into the shell aperture or to remove the epiphragm and probe the snail's foot. By contrast, snails in aestivation for a short duration required a minimum of disturbance to break aestivation. Usually, merely placing dormant snails for a short time in vials resulted in reactivation. Further, in Type II observations I noted that light rain or heavy fog generally was effective in inducing activity in the early part of the summer. Heavy rain, or, in one instance, wind sufficient to knock snails loose from their aestivation sites, was necessary to initiate activity in the late summer.

Differences in drops in population density averaged for 4 years (Table 2) indicated that young of-the-year survive

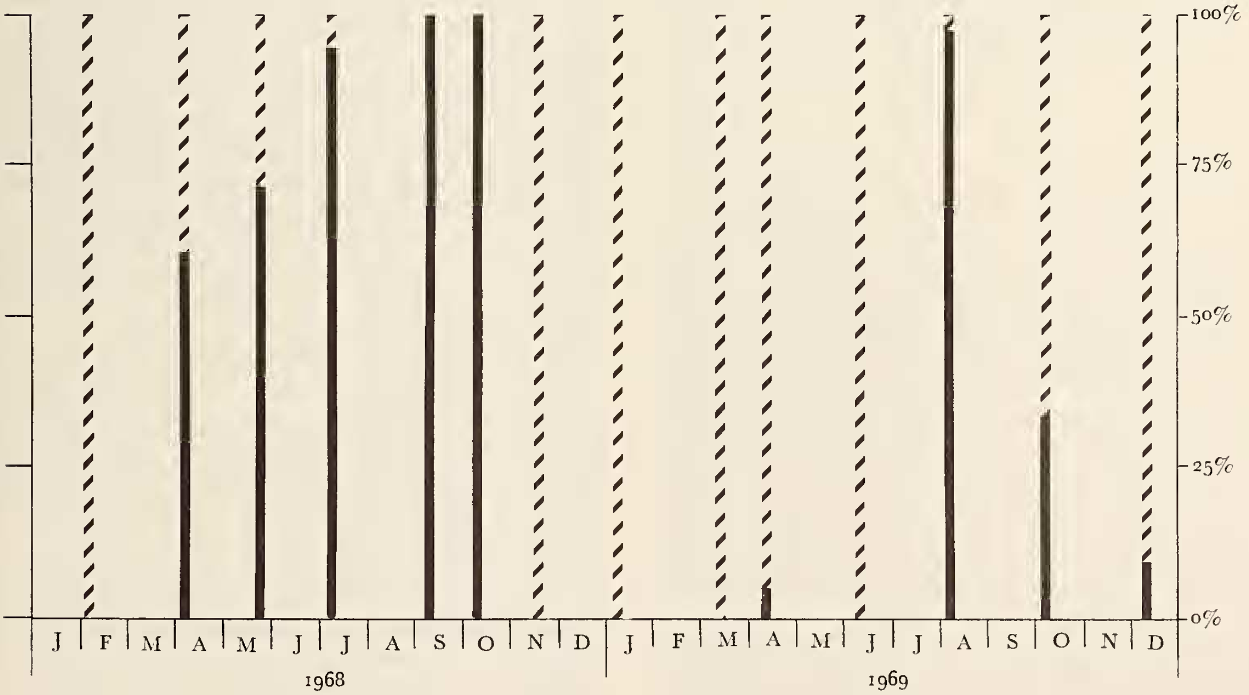


Table 2

The percentage changes in snail population size during time of aestivation (the dry season) and time of activity (the wet season) up to time of annual recruitment averaged for 4 years.

	Time of aestivation starting with when at at least 75% of the population were in aestivation (late May to early August) and ending with time when at least 75% were active (mid-Sept. to mid-November)	Time of activity starting with when at least 75% were active (mid-September to mid-November) and ending with time of annual recruitment (late winter).
Young-of-the-Year	−81%	−25%
Older Snails	−20%	−24%

aestivation less well than older snails and survive times of aestivation less well than times of activity. I noted also that *Helminthoglypta* eggs are not resistant to summer desiccation, for all eggs I collected (Type III) during annual dry periods - late spring to early autumn - were dried out and in some instances cracked open.

DISCUSSION

When the nature, frequency and importance of aestivation of *Helminthoglypta* in the field are compared to aspects of aestivation in other pulmonates, a number of similarities and differences can be noted. As mentioned above, long term dormancy during the dry season as manifested by *H. arrosa* is a widespread phenomenon (Bonavita, 1964; Comfort, 1957; Kondo, 1964; Pomeroy, 1968; Owen, 1965). In addition, as for *H. arrosa*, dormancy following dry periods during what normally would have been the wet season, has been reported for *Helicella virgata* da Costa in Australia (Pomeroy, *op. cit.*). In the Australian study, like *Helminthoglypta*, a seasonal difference in responding to moisture was noted; however, unlike *Helminthoglypta*, a given amount of rain led to a larger proportion of *Helicella* waking the later it was in the dry season. *Helicella*, like *Helminthoglypta*, produced numerous epiphragms, up to 8 or 10, during prolonged aestivation; on the other hand, *Helminthoglypta nickliniana* (Lea, 1838) made 3 epiphragms shortly after (48 and 81 hours) starting aestivation (Ingram, 1943).

In a laboratory study, Wells (1944) found for *Helix pomatia* rain acted as the immediate mechanism of activation after drought, not by hydration of the tissues, but rather by mechanical stimulation. He compared rain drops to "knocks on the door." Responding to rain heavy enough to create mechanical stimulation and requiring a greater amount of rain to reactivate them later in the dry season, rather than lesser amounts as for *Helicella*, makes sense for *Helminthoglypta* living in the northern California coastal climate where the environment becomes progressively drier from mid-June through mid-September. Machin (1964, 1965) and Pomeroy (1968) have shown that water loss is very high in active snails that experience dry conditions. If mere hydration elicited activity, nightly fog or light rain which occurs until mid-August might result in *Helminthoglypta* becoming active during this usually dry period. On the other hand, if rain must be fairly jarring to elicit activation, *Helminthoglypta* will come out of aestivation only after storms that thoroughly wet the environment; the snails will also be insured that, following reactivation, abundant free water would be available for at least a short while.

Following a heavy rain snails are likely able to rapidly gain a net increase in water. In my (see above) and in Howles & Wells' (1934) laboratory experiments recently awakened snails gained 50% weight in less than 24 hours. I have observed *Helminthoglypta* drinking free water and Machin (1964) showed that *Helix aspersa* could absorb free water through its skin. In Australia, *Helicella* appeared to become waterlogged when the ground was saturated with water (Pomeroy, 1968), an observation which I have made also with *Helminthoglypta*. From this fact Pomeroy concluded that *Helicella* also can absorb water through its skin, which is probably true in *Helminthoglypta* also. It has been shown, moreover, that *Helix aspersa* takes up water from the air when the relative humidity exceeds 95% (Machin, *op. cit.*). This ability may generally be present in the helicids.

Rain heavy enough to induce breaks in dormancy not only allows for rapid water uptake by the snails, but it also gives *Helminthoglypta* an opportunity to eliminate metabolic wastes that apparently accumulate during long periods of dormancy. I frequently found unusually long fecal strings which were egested by recently activated *H. arrosa* in the field.

The tendency for juvenile snails to survive aestivation less well than older snails was corroborated by Series B and C. In both these series younger snails, perhaps due to thinner shells and higher surface to volume ratios, tended to die sooner under dry conditions.

Part of the reduction in mortality of older aestivating snails can be attributed to less predation on snails. Predation was reduced in 2 ways: (1) the carabid beetle *Schaphinotus ventricosus* Dejean, which preys on larger snails to the exclusion of small snails (van der Laan, 1971), had a very low abundance during the summer as compared to the rest of the year and (2) since larger snails (14mm+ least diameter) aestivated attached to trunks of bush lupines 20 or 30cm above the ground, larger snails probably escaped the attention of ground dwelling predators such as *S. ventricosus*, deer mice, garter snakes, and alligator lizards (see below for more comments on this behavior of larger snails).

Avoidance of mortality by avoidance of desiccation, however, was probably a more important effect of aestivation than reduction in predation since in summer the environment has the lowest moisture and is the warmest, hence the most desiccating time of the year, and since in Series B and C and in Machin's (1966, 1967, 1968) laboratory studies aestivation and epiphragm formation greatly reduced water loss. In Machin's study (1964, 1965) rate of water loss from mucus on exposed skin was not significantly different from the evaporation rate of distilled water. Pomeroy (1968) also showed for 2 helicid species that a rapid loss in weight occurred with only small activity on a warm day (for example, 15% weight loss after a movement of 12cm after snails were awakened during aestivation).

In addition to summer being a very dry season on Bodega Head, it is a time when food levels sharply decline (van der Laan, 1971: 50; fig. 11). Presumably then, aestivation enables *Helminthoglypta* to have a low energy demand during a season of low food availability. Avoidance of times of low food levels was not entirely complete, however, since snails reactivated in early autumn when food was even scarcer than in summer. On the other hand, scarcity was of short duration since by late autumn food levels rapidly increased.

SELECTION of AESTIVATION SITES

I observed that *Helminthoglypta* selected aestivation sites that were out of direct sunlight, thus avoiding a great deal of desiccation. The location of *H. arrosa*'s aestivation site varied with the size of the snails. Snails less than 3mm LD were under the tangle of vegetation made by *Chenopodium californicum* (Watson) Watson, *Marah fabaceus* (Nandin) Greene, *Amsinckia Menziesii* (Lehm) Nelson & Macbride, *A. spectabilis* F.&M., *Phacelia distans* Bentham, and dead *Lupinus* branches. Larger snails were also found aestivating under the vegetation, but as the size of the snails increased to around 9mm LD, most snails used mucus and attached themselves by their apertures to twig surfaces. As mentioned above, animals larger than 14mm LD were attached to bush lupine. The smaller of the large snails frequently were found on lupine stems on the ground, but larger snails in this size class were found 20 to 30cm above the ground, on the lupine trunks and stems.

I hypothesized that the lupine aestivation site was selected by the larger *Helminthoglypta* for one or more of the following reasons: (1) Because of the immobility associated with aestivation, snails very likely were vulnerable to predation during dormancy, but by aestivating above the ground the large snails might be sufficiently removed from the attention of the ground dwelling predators. The notion that snails escape predation by climbing has previously been suggested by Blinn (1963). He observed that the pulmonate *Mesodon thyroidus* Say, 1816, especially the younger snails, climb trees. Unfortunately, Blinn presented no direct evidence for his conclusion. Unlike *H. arrosa*, this climbing occurred during seasons when *Mesodon* were active. (2) Larger *H. arrosa* may climb up lupine stems to gain flat surfaces large enough to completely cover the shell aperture. Perhaps complete closure is necessary for adequate attachment to the substrate or complete closure makes a more complete seal against desiccation. Such surfaces are scarce in the leaf litter, but the trunk of *Lupinus* is wide enough to cover the aperture. (3) Finally, following the reasoning of Pomeroy (1968), who studied Australian *Helicella virgata* which aestivate on open posts, it is possible that the lupine sites provided a better microclimate over that provided on the ground.

EFFECTS of MICROCLIMATES

To test if the lupine site provided a better, or even a different, microclimate than on the ground, I measured the relative humidity, temperature, and wind velocity in the leaf litter, under the canopy of the lupine leaves next to the lupine's main trunk, and 1m above the ground in the shade of my body. Measurements of relative humidity and temperature were taken every 6 hours over a 24 hour period on 13-14 February and 8-9 May, 1968, when ambient conditions were dry. Ambient conditions were dry and there was a 30km/hr wind blowing when air speed was estimated on 20 March, 1970.

The results indicate no special microclimatic advantage to the lupine aestivation site. Temperatures and relative humidity for the various microhabitats were nearly the same. For example, the most varied results for 13-14 February ranged over 59.0 - 61.9% relative humidity and 13.8° - 16.6° C and for 8-9 May, 52.2 - 55.0% relative humidity and 16.6° - 18.9° C. Other estimates ranged less than 4% relative humidity and 2° C. Wind velocity was lowest just under the top of the prostrate vegetation

(0.2 km/hr), next lowest above the ground level (0.2 to 0.6 km/hr); at the height (20 - 30 cm) on the lupine trunk where larger snails aestivated, wind velocity was even higher (0.8 - 2.3 km/hr) and thus more desiccating than near the ground. In addition to measurements of microclimate I noted that following dews and light rains during the dry period, both lupine trunks and the soil under the prostrate vegetation remained dry. I reject, therefore, the possibility that the lupine trunk was less desiccating than the leaf litter or that the trunk provided protection from extremes in temperatures and hydration which, as in Pomeroy's study, might induce reactivation at a time when food was scarce.

EFFECTS of POTENTIAL SIZE of AESTIVATION SITE

To test if larger snails select surfaces large enough to cover shell apertures I presented equal surface areas of 2 sizes of wooden dowels (3.2 mm in diameter - larger than aperture size; and 1.1 mm - smaller than aperture size) which were stuck vertically in sand, to a group of recently activated adult snails and proved that *Helminthoglypta* does select larger surfaces over smaller surfaces for aestivation sites (Table 3). In these experiments I further showed that when adult snails found large enough surfaces, they climbed up them.

A large proportion of the snails in these experiments began aestivation well above the sand surface on the framework of a cage that was placed over the dowels and sand. The framework of the cage was wider (2.5 cm) than either of the dowels. Just considering the snails that selected dowels for aestivating sites, I found that the actual proportion of large dowels that the snails selected was significantly different from a 50 : 50 pick of dowels (Table 3). In an earlier experiment the snails also disproportionally picked larger dowels over smaller ones, but the snails were presented equal numbers of each dowel size, not equal areas for each size. Hence, I consider the earlier results inconclusive when considered alone, but lending support to my conclusions when considered with the later results.

Table 3

The recorded positions summed for 7 trials of adult snails placed in a wire enclosure (1 m³) and presented different sized dowels placed vertically in sand.

	Large Dowels (.32 cm in Diameter)	Small Dowels (.11 cm in Diameter)	Sand	Cage Framework (2.5 cm in Width)
Sum of 7 24-hour Trials	17	7	41	32
Numbers expected with a 50-50 pick of dowels	12	12		

Chi-square = 4.2
Significant at 5%

The selection of some surfaces smaller than shell apertures by *Helminthoglypta* in the laboratory (a field observation also made for *Helicella*, Pomeroy, personal communication) indicates that complete aperture coverage may not always be critical. On the other hand, I never observed less than the whole aperture covered during prolonged - 1 week or more - aestivation in the field.

EFFECTS of PREDATORS

The fact that the large snails were shown to select larger surfaces over smaller ones for aestivation sites does not negate the additional possibility that *Helminthoglypta* aestivates on the lupines to avoid predation. In fact, I made observations in the field and in the laboratory that show that snails escape predation by climbing up from the ground.

From 1 January, 1968 to 31 January, 1969, I monitored the survival of individually marked adult snails confined in 10 1 m³ wire mesh cages in the field. During the experiment 20 out of 33 snails disappeared or their empty intact shells were found. I assume that mortality accounts for the disappearance. When I noted that a snail was missing, I immediately searched the area around the cage. Furthermore, for another part of my study, I periodically observed and noted active snails near the cages, especially marked snails. Snails that were missing from the cages were never found.

Since it has been shown that adult *Helminthoglypta* have a longevity of over 4 years (van der Laan, 1971, 1975b), I consider the high mortality rate of the caged snails to be quite high when compared to the general snail population on Bodega Head and therefore peculiar to caged snails. Lack of food in the cages cannot be a factor in this high mortality rate since there was an abundance of the snail's preferred foods, determined earlier (van der Laan, 1975a). Likewise, desiccation from high temperatures or lack of moisture cannot account for the high mortality. Each of the cages was in the shade of a bush lupine, and many deaths and disappearances occurred during the wet season. It is significant, however, that no lupines were within the cages and that snails aestivated on the bottom cage framework rather than the upper framework. I believe therefore that the disappearances and deaths are due to exposure to ground dwelling predators: the deer mouse *Peromyscus maniculatus* Wagner, the garter snake *Thamnophis sirtala,* the northern alligator lizard *Gerrhonotus coeruleus* Wiegmann and the carabid beetle *Scaphinotus.*

Further proof that climbing saves aestivating *Helminthoglypta* from predation came from experiments conducted in the laboratory. When confined with *Scaphinotus* and *Peromyscus*, adult-sized snails on container floors were attacked, but the snails that crawled only a short distance (2 - 3 cm) up the container walls and commenced aestivation, were not molested.

If climbing during aestivation indeed leads to reduced predation, why then don't all sizes of snails climb? In the laboratory observations mentioned above I noted that *Scaphinotus* never attacks snails less than 10 mm LD; thus predation pressure on smaller snails is partly relieved. In addition, it has been found that *Helminthoglypta* less than 10 mm LD have a low vagility: a maximum daily horizontal movement of 7 cm during the wet season and 1 - 2 cm during the dry season (van der Laan, 1971: 115; table X). By comparison, larger snails (>10 mm LD) moved 13 to 50 cm per day. The exact reasons for differences in vagility remain unknown, although they probably relate to food or water supply. I speculate that the depletion of food or water reserves necessary to travel up lupine trunks places the smaller snails at greater risk than avoidance of predation by climbing, thus accounting for their absence on lupine trunks.

SUMMARY

In a four year study (March, 1966 to December, 1969) *Helminthoglypta arrosa*, a terrestrial pulmonate that inhabits a lupine scrub stand, *Lupinus arboreus,* on Mussel Point, Bodega Head, Sonoma County, California, had a high occurrence - greater than 70% of the total number of animals collected - of aestivation during the drier months, mid-May to early October. Generally, all snails were in aestivation in July and August of each year and no snails were in aestivation from January to March.

In the laboratory it was found that resistance to desiccation depended on a vital process and that during aestivation the epiphragm, a dried mucus sheath secreted by the snail's foot at the shell aperture, was important in reducing weight loss. In the laboratory, aestivating snails can survive relative humidity of <5% for long periods of time - 170+ days. Probably due to thicker shells and lower surface to volume ratios: (1) in the laboratory at a relative humidity of <5% larger animals tended to survive longer than smaller animals and (2) in the field during summer dormancy larger animals had lower mortality rates than during time of activity (20% compared to 24%), whereas smaller animals had mortality rates that were higher than larger snails (81%) and that were higher at times of activity (25%). As an adaptation to increasingly more desiccating conditions during the dry season, with prolongation of aestivation, (1) snails were farther withdrawn into their shells, (2) 2 or 3 epiphragms rather than 1 epiphragm were likely to be formed, and (3) stimulation - rain, jarring and handling - sufficient to induce reactivation needed to be more intense. Avoidance of starvation during times of low food supply is probably an important effect of aestivation; however, avoidance of desiccation is probably a more important effect. The smallest snails aestivated under the tangle of vegetation and larger snails attached themselves by their apertures to twig surfaces. The largest snails aestivated 20 or 30 cm above the ground on lupine trunks and stems. Differences in microclimates were eliminated as an explanation for this variation in selection of aestivation sites. In the laboratory, larger snails selected larger surfaces over smaller surfaces as aestivation sites, indicating that flat surfaces large enough to completely cover the shell aperture, which in the field are only provided by *Lupinus*, are a prerequisite to aestivation. In addition, there are strong indications that by aestivating above the ground surface the largest snails avoid the attention of the ground dwelling predators: the deermouse *Peromyscus maniculatus*, the garter snake *Thamnophis sirtala,* the northern alligator lizard *Gerrhonotus coeruleus*, and a ground beetle *Scaphinotus ventricosus.*

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